A STUDY OF ALLELOPATHY IN

HELIANTHUS RIGIDUS

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CHAPTER I

INTRODUCTION

There are many factors that contribute to a plant's success or failure in a certain community. One of these factors is interference, which can be further broken down into competition and allelopathy. Competition is here defined as the depletion of some necessary factor by an individual or population to the detriment of some other individual or population sharing the same habitat. Allelopathy, on the other hand, is the release into the environment of a chemical compound which has deleterious effects on individuals or populations in the same or neighboring havitat (Muller 1969, Rice 1974). Many workers have assumed that the failure of a species to move into a seemingly favorable habitat was due to competition, without making the experiments necessary to determine if the reason is competition or allelopathy or some combination of the two, or some naturally occurring physical environment extreme. It is therefore the responsibility of the researcher to prove that allelopathy or competition is the cause of the apparent inhibition (Muller 1969, Muller 1974).

Allelopathy plays a role of some degree in many of the traditionally recognized processes of plant ecology. If a species can exclude another species from a habitat, then competition between the two species never occurs. Dominance of a community can be achieved either through allelopathy or competition or a combination of the two. Secondary succession

often involves allelopathy as well as competition. Autointoxication is particularly suited to the rapid decline of a species in a community, thus enabling other species to become established and accelerating the successional series. Also, if an invading species is more effective at inhibiting previous occupants than inhibiting itself, succession occurs. Another effect of allelopathic chemicals is that they tend to reduce productivity (Muller 1969, Muller 1974).

Muller (1966) found that Salvia leucophylla shrubs produce several volatile terpenes which are toxic to the grassland species found in the California grasslands. There is a bare zone extending beyond the shrubs followed by area of three to eight meters wide of stunted grassland species. Bioassays showed that the volatile terpenes were inhibitory to the seed germination and radical growth. Muller suggested that the autointoxication of the Salvia, causing deterioration of old stands, could be a significant factor in plant succession.

McPherson and Muller (1969) showed that the absence of herbaceous species in mature Adenostoma fasciculatum stands was due to the release of several water soluble phenolic acids which are toxic to seed germination and radical growth. These phenolic acids are released to the leaf surface, washed off by the rainfall and accumulated in the upper few centimeters of soil, where they effectively suppress the germination and growth of herbaceous species.

Allelopathy is known to be present in some species of Helianthus, but studies of the genus have not been extensive. The two species that have been investigated are Helianthus annuus and Helianthus rigidus, with H. annuus being the most intensively studied. Helianthus annuus was studied by Wilson and Rice (1968) while H. rigidus was investigated by Cooper and Stoesz (1931) and by Curtis and Cottam (1950).

Wilson and Rice (1968) investigated the allelopathic properties of the weedy annual H. annuus and its role in old field succession. They examined extracts of leaves, young inflorescences, roots and stems, decaying leaves, exudate of roots, leaf leachate and soils near the H. annuus plants for indications of allelopathy. They found that seed germination and seedling growth of H. annuus and six other associated species were inhibited, but that Aristida oligantha and Croton glandulosus were not affected. The field study of these species showed strong correlation with the laboratory experiments. From the extracts of the various organs, the phytotoxins chlorogenic acid and isochlorogenic acid were isolated. From the leaf leachate, a suspected α-napthol derivative and scopolin were isolated. The compounds in the soil and root exudate were not identified.

While Helianthus annuus is an annual which occurs in highly disturbed sites, H. rigidus is a perennial which occurs in stable prairie sites. In Weaver and Fitzpatrick's (1934) very extensive study of the Nebraska prairie, they visually ranked the forbs in importance and abundance in the 135 study sites. Helianthus rigidus was the second most important forb, occuring in all but 13 percent of the upland prairie and in 51 percent of the lowlands. Its habitat was typically the uplands and often the distribution was uniform over a large area. The density varied from 100 plants/m^2 when abudant to none, with 40-50 being the most common, but they were never densely clustered. The authors attributed the H. rigidus success to it firbrous roots which compete effectively with the grasses.

Cooper and Stoesz (1931) were investigating the cause of a

Helianthus rigidus[1] clone "fairy ring" in the vicinity of Anoka, Minnesota. (A fairy ring is the phenomenon of a ring of luxuriant vegetation.) They did not believe that water was a factor, since the soil was sandy and water could move quite freely. They tested the theory that there was a chemical addition or depletion which was the cause. In the greenhouse they grew wheat and common sunflower in soil obtained outside the ring, within the area of highest density of plants, within the area of tallest plants, and the center of the ring where there were few individuals. They found a great reduction in the size of the test plants grown in the soil from the tallest area and from the center, but the ones grown in the soil from the highest density of plants were larger than those grown in the soil from the outside. Although they still were not sure of the cause the experiments suggested a chemical cause.

Curtis and Cottam (1950) investigated the autotoxic effect of Helianthus rigidus. They had a series of four plots within the clones with which they tested the addition of fertilizer, or new soil, and removal of roots and rhizomes. They measured the results in terms of flowering percentage of Helianthus rigidus. There was a significant difference between the control and the two soil alterations, while there was no difference between the control and the fertilized plot. Their experiment thus ruled out competition for nutrients as a causative factor. On the basis of field observations and soil replacement treatment, they were able to dismiss competition for water as well. They

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[1]By them called H. scaberrimus. It appears from the literature (Curtis and Cottam 1950, Heiser et al. 1969) that this taxon is best referred to as H. rigidus.

speculated that the inhibitive substance was stable and was released by the decomposition of the old plant parts.

In any allelopathic work, there are several requirements that must be met in order to establish allelopathy. They are: (a) a toxin must be produced; (b) mean of release of movement and of concentration of the toxins must be identified; (c) susceptibility of inhibited plants must be established; and (d) elimination and/or role of physical and non-chemical factors must be established (Muller 1974).

Although Cooper and Stoesz (1931) and Curtis and Cottam (1950) hinted at the allelopathic potential of Helianthus rigidus, neither group investigated this possibility intensively. This research attempted to carefully evaluate competition, and to investigate several aspects of allelopathy. The distribution of plants in relation to Helianthus rigidus clones was investigated.

The major goals of this research was to determine the role of Helianthus rigidus in the plant community and to study the mechanisms, particularly allelopathy, that exclude some species from the clones.

CHAPTER II

DESCRIPTIONS

Sites Descriptions

The three study sites were located in non-climax communities. At each site there were species present which could be considered weedy annuals, weedy perennials, near climax and climax species. The Helianthus rigidus clones occupied a minimum area of 100 m^2.

The sites were located 6.4 km north and 6.4 km east of the junction of highways 177 and 160 (NW¼ Sec. 9 T20N R3E) (East Clone), 9.6 km north and 3.2 km east of junction of highways 177 and 160 (NE¼ Sec. 36 T 21 N R2E) (North Clone) and at Lake Carl Blackwell (SW¼ Sec. 17 17 T1 9N R1E) (West Clone) in Oklahoma. The East clone and North clone were located in roadside ditches.

Species Description

Heiser et al. (1969) reviewed the taxonomic descriptions and related information of the genus Helianthus.

Helianthus rigidus (Cass.) Desf., roughleaf or stiff sunflower, is a perennial sunflower 0.3-2.0 m tall. Helianthus rigidus begins growth in the early spring from tubers formed the previous year. On the mature plant generally the upper 4 or 5 pairs of leaves remain green while the lower ones usually die and remain on the plant. Helianthus rigidus propagates mainly by tubers. The tubers are formed at the ends of

rhizomes which radiate from the base of the plant. Each plant produces one to several rhizomes which range up to 100 cm in length. By September, the tubers have developed a root system similar to the parents except the rootlets are lacking. Helianthus rigidus is readily eaten by livestock, but it cannot withstand grazing well, hence it is usually found only where the area has been protected from grazing (Weaver 1954, Cooper and Stoesz 1931).

CHAPTER III

VEGETATION ANALYSIS

Methods of Study

The Helianthus rigidus clones were observed to have fewer weedy species than the surrounding area. To quantify these observations, the vegetation within and surrounding the clones were sampled using a quadrat of 20 cm by 25 cm divided into five subquadrats by 5 cm by 20 cm. In May, the vigor was determined by measuring the height of an individual of each species within each subquadrat closest to a randomly selected point. In August, the vegetation was sampled using the same quadrat with the biomass being determined by clipping the subquadrats at ground-level, oven-drying at 105 C for 24 hours, and weighing to the nearest 0.01 g. A minimum of ten quadrats were used at each clone during both sampling periods. The samples were randomly located within and around the clones. An individual was defined as a shoot consisting of a stem and all its appendages.

Results and Discussion

Tables I and II show frequency, density, and vigor of each species in relation to Helianthus rigidus frequency. Due to the small number of individuals of several species encountered during sampling, many of the large differences in frequency, density, height and biomass were not statistically significant. Even though the differences were not

statistically significant, they were biologically significant.

A total of 28 species were encountered during the spring sampling (Table I). The greatest number of species occurred when the H. rigidus frequency was 0. The presence of any H. rigidus substantially diminished the number of other species present, however greater densities of H. rigidus showed little tendency to further reduce other species. The species not found in the clones were Sorghum halepense[1], Chaerophyllum tainturieri and two unidentified forb species and Erigeron philadelphicus was not found when the H. rigidus freqency increased above 20. Of the 18 non-climax species, only five were recorded when the H. rigidus frequency was 100 and either their frequency, density or height decreased as the frequency of H. rigidus increased. In general, the increase in frequency of H. rigidus did not have much effect on the climax species.

A total of 19 species were encountered during the fall sampling (Table II). The greatest number of species occurred where there was no H. ridigus. Of the 12 non-climax species present outside the clones. five were found within the clones. Of the weedy species, only Digitaria sanguinalis was found when the frequency of H. rigidus was 80 but Digitaria made up only a small part of the vegetation. Only climax species were found when the H. rigidus frequency was 100. In general, the presence of H. rigidus increased the frequency, density or vigor of the climax species and decreased weedy species.

Combining the results of the spring and fall sampling the species not found in the H. rigidus clones were Sorghum halepense, Chaerophyllum

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[1]Nomenclature follows Waterfall, 1969, unless authority is given.

tainturieri, Gutierrezia dracunculoides, Andropogon saccharoides and two unidentified species. The species found in areas of low H. rigidus frequency ($\leq$40) were Sisyrinchium angustifolium, Eragrostis trichodes, Achillea lanulosa, Sporobolus cryptandrus and Erigeron philadelphicus.

TABLE I

FREQUENCY (FREQ), DENSITY (DEN), AND HEIGHT (HT) OF SPRING SAMPLED SPECIES AT THE SITES AS A FUNCTION OF HELIANTHUS RIGIDUS FREQUENCY

Type[1]	Species		H. rigidus freq.					
			0(n=7)[2]	20(n=4)	40(n=6)	60(n=6)	80(n=5)	100(n=8)
C	Helianthus rigidus	freq[3]		20	40	60	80	100
		den[4]		20	50	100	136	160
C	Andropogon gerardi	freq	3	10	10			
		den	3	50	13			
		ht[5]	100	97	83			
C	Andropogon scoparius	freq	29		20	7		8
		den	103		113	17		73
		ht	100		66**	57**		71*
C	Psoralea tenuiflora	freq	31	30	10	7	5	15
		den	40	45	10	10	12	25
		ht	100	125	140	80	45	35
C	Panicum virgatum	freq	3	20				5
		den	3	70				15
		ht	100	91				105
C	Sorghastrum nutans	freq	3					5
		den	9					8
		ht	100					142

TABLE I (Continued)

Type[1]	Species		H. rigidus freq.					
			0(n=7)[2]	20(n=4)	40(n=6)	60(n=6)	80(n=5)	100(n=8)
C	Schrankia uncinata	freq	11	10				5
		den	11	10				8
		ht	100	68				72
C	Trifolium spp.	freq	9	25		13		
		den	9	70		27		
		ht	100	80		100		
C	Desmodium spp.	freq			3			8
		den			3			18
C	Panicum oligosanthes var. Scribnerianum	freq	3			3	8	
		den	3			3	24	
		ht	100			31	44	
NC	Tridens flavus	freq	9				12	
		den	9				16	
		ht	100				16*	
NC	Andropogon ternarius	freq	29	30	37	20		15
		den	177	90	247	90		25
		ht	100	47	106	26		126
WP	Sisyrinchium angustifolium	freq			3			
		den			3			
WP	Artemisa ludoviciana	freq			3	3	4	10
		den			3	3	4	13

TABLE I (Continued)

Type[1]	Species		H. rigidus freq.					
			0(n=7)[2]	20(n=4)	40(n=6)	60(n=6)	80(n=5)	100(n=8)
WP	Achillea lanulosa	freq			3			
		den			3			
WP	Ambrosia psilostachya	freq	17		7		12	5
		den	17		10		12	5
		ht	100		119		81	38
WP	Sporobolus cryptandrus	freq	3		3			
		den	3		3			
		ht	100		158			
WP	Sorghum halepense	freq	3					
		den	3					
WP	Erigeron philadelphicus	freq	5	10				
		den	5	10				
		ht	100	140				
WP	Oxalis spp.	freq	11		7	8		
		den	31		7	16		
		ht	100		100	100		
WP	Croton spp.	freq	17	5	10	20	8	3
		den	26	10	17	23	20	3
		ht	100	60	290	230	90	220
WP	Convolvulus spp.	freq	14	20	7	10	8	3
		den	31	20	10	13	8	5
		ht	100	65	70	100	83	22

TABLE I (Continued)

Type[1]	Species		H. rigidus freq.					
			0(n=7)[2]	20(n=4)	40(n=6)	60(n=6)	80(n=5)	100(n=8)
WA	Cassia fasciculata	freq	11	20		13	28	
		den	14	30		17	32	
		ht	100	214		114	61	
WA	Chaerophyllum tainturieri	freq	9					
		den	9					
WA	Digitaria sanguinalis	freq	11	10	10	7	4	
		den	49	10	30	7	12	
		ht	100	53	100	63	53	
	Others (3 species)	freq	23	10		3		
		den	32	10		3		
		ht	100	29		17		
Number of Climax species at each frequency			8	6	5	5	3	7
Number of Non-climax species at each fequency			12	6	10	7	7	5
Total number of species at each frequency			20	12	15	12	10	12

TABLE I (Continued)

[1] C = Climax species
NC = Near climax species
WP = Weedy perennial species
WA = Weedy annual species

[2] Number of quadrats

[3] $\text{Frequency} = \frac{\#\text{ of subquadrats species found in}}{\#\text{ of subquadrats}} \times 100$

[4] $\text{Density} = \frac{\#\text{ of individuals}}{0.05\ m^2 \times \#\text{ of quadrats}}$

[5] $\text{Height} = \frac{\text{average height}}{\text{average height at O } \underline{\text{H. rigidus}} \text{ freq.}} \times 100$

*$p < 0.05$ by t-test

**$p < 0.01$ by t-test

TABLE II

FREQUENCY (FREQ), DENSITY (DEN), AND BIOMASS (BIO) OF FALL SAMPLED SPECIES AT THE SITES AS A FUNCTION OF HELIANTHUS RIGIDUS FREQUENCY

Type[1]	Species		H. rigidus freq.					
			0(n=17)[2]	20(n=0)	40(n=7)	60(n=2)	80(n=4)	100(n=2)
C	Helianthus rigidus	freq[3]			40	60	80	100
		den[4]			80	160	155	130
C	Andropogon gerardi	freq	1		14		5	
		den	3		77		20	
		bio[5]	100		173		68	
C	Andropogon scoparius	freq	30		23	40	35	30
		den	161		257	100	125	280
		bio	100		75	54	96	42
C	Sorghastrum nutans	freq	15		26	20	30	
		den	67		111	130	125	
		bio	100		52	40	25	
C	Schrankia uncinata	freq	1					20
		den	1					40
		bio	100					406
C	Eragrostis trichodes	freq			3			
		den			17			
C	Panicum oligosanthes var. Scribnerianum	freq	13		3			
		den	33		6			
		bio	100		128			

TABLE II (Continued)

Type[1]	Species		H. rigidus freq.					
			0(n=17)[2/]	20(n=0)	40(n=7)	60(n=2)	80(n=4)	100(n=2)
NC	Tridens flavus	freq	6					
		den	15					
NC	Bouteloua curtipendula	freq					20	
		den					100	
NC	Andropogon ternarius	freq	5					
		den	29					
WP	Artemisa ludoviciana	freq	3		6			
		den	3		6			
		bio	100		10			
WP	Ambrosia psilostachya	freq	31		9	10		
		den	29		11	20		
		bio	100		108	60		
WP	Sorghum halepense	freq	6					
		den	15					
WP	Andropogon saccharoides	freq	10					
		den	49					
WP	Croton spp.	freq	8					
		den	9					
WA	Cassia fasciculata	freq	4					
		den	4					

TABLE II (Continued)

Type[1]	Species		H. rigidus freq. 0(n=17)[2]	20(n=0)	40(n=7)	60(n=2)	80(n=4)	100(n=2)
WA	Digitaria sanguinalis	freq	6		11		5	
		den	16		46		35	
		bio	100		111		133	
WA	Aristida oligantha	freq	13		3	20		
		den	149		74	50		
		bio	100		138	25		
WA	Gutierrezia dracunculoides	freq	6					
		den	6					
Number of climax species at each frequency			5		6	3	4	3
Number of non-climax species at each frequency			11		4	2	3	0
Total number of species at each frequency			16		10	5	7	3

[1] C = Climax species
NC = Near climax species
WP = Weedy perennial species
WA = Weedy annual species

[2] Number of quadrats

[3] $\text{Frequency} = \frac{\text{\# of subquadrats species found in}}{\text{\# of subquadrats}} \times 100$

[4] $\text{Density} = \frac{\text{\# of individuals}}{0.05\ m^2 \times \text{\# of quadrats}}$

[5] $\text{Biomass} = \frac{\text{average weight/individual}}{\text{avg. wt./individual at 0 H. rigidus freq.}} \times 100$

*$p < 0.05$ by t-test

**$p < 0.01$ by t-test

CHAPTER IV

COMPETITIVE FACTORS

In any study involving allelopathy, the researcher has the responsibility to clearly establish the role, if any, of competition for physical factors (Muller 1974). Three physical factors, which could possibly be limiting and prevent some species from growing in a Helianthus rigidus clone, were investigated. At each site light, soil moisture, and soil nutrients were measured within and outside the clones to determine if they were limiting within the clone.

Light

Light measurements were collected at two-week intervals between 1 July and 1 August. At each site a 5 m transect was established within a Helianthus rigidus clone and another in the surrounding vegetation. The readings were taken every 10 cm with a Weston Illumination Meter Model 756. At each point, three readings were taken 30 s apart to determine the average reading.

Light readings were collected on sunny, cloudless days between 1130 and 1630 hr CST. The same order of collecting was followed during each collection period. All readings were collected at ground level or at the mulch layer surface. The same procedure of collection was used for each site. Full sunlight was taken at each site.

Table III shows the average light intensity at each site within

a Helianthus rigidus clone and in the surrounding vegetation. The full sunlight readings were all greater than 12,000 fc. At two sites, the light intensity is significantly higher ($p < 0.001$) and the third was 500 fc higher within the Helianthus rigidus clone than the surrounding vegetation.

TABLE III

AVERAGE LIGHT INTENSITY (FC) WITHIN (IN) AND OUTSIDE (OUT) OF A HELIANTHUS RIGIDUS CLONE BY SITE

Site	In	Out
East Clone	8398[a,1]	6880[a]
North Clone	5201[b]	1867[b]
West Clone	5005	4505

[a-b]Duplicated superscript letter indicates significant difference ($p < 0.001$ by F-test) between each pair.

[1]n=150 for each value

Soil Moisture

Soil moisture determinations were made every two weeks during the period 25 June-18 August. At each site six areas were selected, three within the clone and three outside the clone in the same vicinity. Topography and aspect of the clone area were paired with the non-clone area. Soil samples were collected with a geotome at the depths of 2-10 cm

TABLE IV

PERCENT SOIL MOISTURE AT 2-10 CM AT VARIOUS TIMES WITHIN (IN) AND OUTSIDE (OUT) OF A HELIANTHUS RIGIDUS CLONE BY SITE

Site	East Clone		North Clone		West Clone	
	In	Out	In	Out	In	Out
25 June	14.19	12.18	23.58[b]	21.77[b]	21.16	19.95
7 July	16.31	13.28	15.90	16.50	13.43	13.17
21 July	8.27	6.10	8.38	11.21	8.38	9.49
4 August	11.22	4.70	9.53	12.22	16.69	16.49
18 August	13.13	10.82	19.96	19.40	11.80	11.94

[a-b]Duplicated superscript letters indicate significant difference ($p < 0.05$ by F-test) between each pair.

TABLE V

PERCENT SOIL MOISTURE AT 20-30 CM AT VARIOUS TIMES WITHIN (IN) AND OUTSIDE (OUT) OF A HELIANTHUS RIGIDUS CLONE BY SITE

Site	East Clone		North Clone		West Clone	
	In	Out	In	Out	In	Out
25 June	21.94	16.98	13.92	10.25	18.23	16.13
7 July	19.77	18.17	19.39	15.13	19.33	20.42
21 July	16.44	12.41	13.77	10.52	15.77	14.61
4 August	17.37	13.60	12.71	10.11	16.59	16.06
18 August	18.45	15.10	16.41	13.73	15.78	15.61
Average	18.79[a]	15.25[a]	15.24[b]	11.95[b]	17.14	16.57

[a-b]Duplicated superscript letters indicate significant difference ($p < 0.05$ by F-test) between each pair.

and 20-30 cm. A sample consisted of three cores of a given depth taken at random points within each area. Soil samples were placed in standard aluminum soil sample cans, returned to the laboratory and weighed to the nearest 0.01 g. Samples were dried at 105 C for 72 hours in a forced air oven and percent soil moisture was determined gravimetrically.

Percent soil moisture at 2-10 cm and 20-30 cm at the collection times within and outside the Helianthus rigidus clone at each site is presented in Table IV and V. The east clone had significantly ($p < 0.05$) more soil moisture at 2-10 cm than the surrounding area while the other two sites had very similar percent soil moisture at 2-10 cm. At 20-30 cm the percent soil moisture was significantly greater ($p < 0.05$) in two clones and slightly higher in the other, than in their respective surrounding areas.

Soil Nutrients

The presence of sufficient soil nutrients was determined once during the 1977 growing season. At each site a soil sample was collected within the clones and outside the clone in the same area as the clone sample. The soil samples were dried at 105 C for 72 hours, sifted through a 2 mm sieve and mixed. In small plastic pots 10 wheat seeds were planted in 400 g of soil. After germination the wheat was thinned, leaving the five largest plants per pot. There were ten replicates of each treatment randomly arranged on aluminum trays. The trays of pots were placed under a photobank with a 15-9 hour light-dark regime and were watered by subirrigation as needed. After eleven weeks, the plant tops were removed at ground level, oven dried for 24 hours at 105 C and weighed to the nearest 0.01 g.

Table VI shows the average dry weight per pot (5 plants/pot) of wheat plants grown in soil from a Helianthus rigidus clone and from the area outside the clone. Wheat grown in soil from two clones were significantly heavier ($p < 0.05$, $p < 0.01$) and slightly heavier in the other clone than the wheat grown in the soil from surrounding area. The average weight of wheat grown in Helianthus clone soil was significantly higher ($p < 0.01$) than the wheat grown in soil from surrounding area.

Discussion

Competition for the physical factors of light, soil moisture, and soil nutrients have been strongly indicated not to be limiting factors in determining the distribution of species within the sites. These factors are in as great or greater abundance within the Helianthus rigidus clone as the surrounding area. Thus, competition for these physical factors are not preventing the species not found within the clones from growing there.

TABLE VI

AVERAGE DRY WEIGHT PER POT (5 PLANTS/POT) OF WHEAT PLANTS GROWN IN SOIL FROM WITHIN (IN) AND OUTSIDE (OUT) OF *HELIANTHUS RIGIDUS* CLONES

Site	In	Out
East Clone	0.578[1]	0.532
North Clone	0.556[a]	0.437[a]
West Clone	0.715[b]	0.587[b]
Average	0.616[c]	0.519[c]

[a]Duplicate superscript letters indicate significant difference ($p < 0.05$ by F-test) between pairs.

[b-c]Duplicate superscript letter indicate significant difference ($p < 0.01$ by F-test) between pairs.

[1]n=10 for each value

CHAPTER V

ALLELOPATHY

Bioassay

Methods of Study

Laboratory bioassays for allelopathic substances production and release by the green shoots, living roots, dead roots, litter and dead leaves remaining on the living shoots of H. rigidus were run each month for twelve months when the material was present. The bioassay procedure used in this study was modified from McPherson and Muller (1969). The leachates were prepared from freshly collected material which was soaked in distilled water in a ratio of 1 g of fresh material to 10 ml of distilled water for three hours in the dark. The leachate was then filtered and used for the experiment.

The test species selected were Achillea lanulosa, a weedy biennial dicot, Andropogon scoparius, a climax grass, and Bromus japonicus, a weedy annual grass. Achillea lanulosa and Bromus japonicus were selected to study the affects of the Helianthus rigidus leachates on weedy species. Andropogon scoparius was selected to study the affects of the leachates on a climax species. These species were also selected for their relative high germination rates and relative ease of germination.

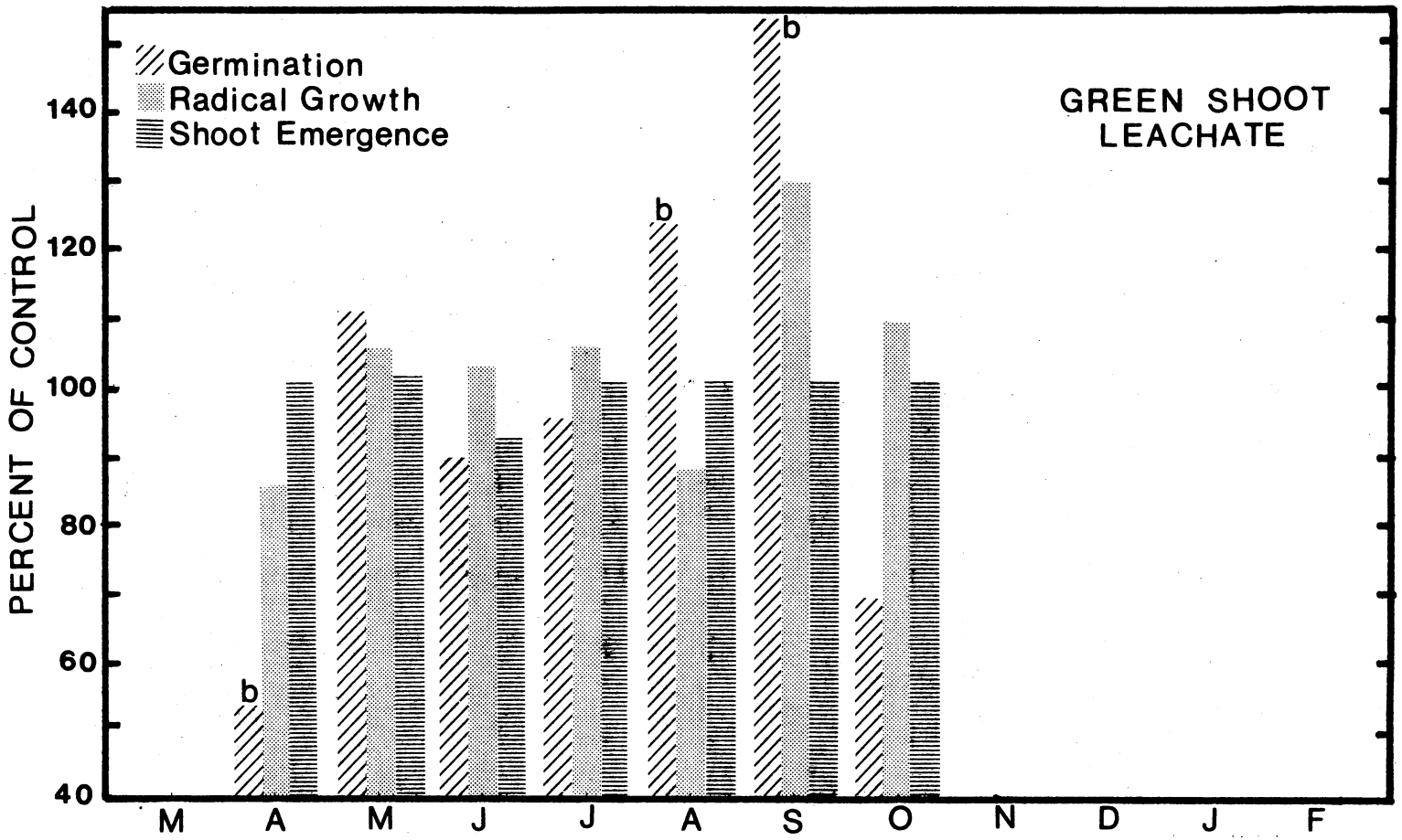
Seeds of the test species; Achillea lanulosa, Andropogon scoparius, and Bromus japonicus, were placed in pertri dishes (100 x 15 mm) containing 70 g of river sand that had been washed, dried and sifted through a 2 mm sieve. Each dish was irrigated with either 10 ml of leachate or 10 ml of distilled water (control), sealed with plastic wrap, and given the appropriate treatment for germination. Achillea was placed directly under a photobank with a 12-12 hour light-dark regime at 23 ± 3 C. Bromus and Andropogon were stratified at 4 C for 17 hours and two weeks respectively then placed under the photobank. After a week under the photobank the percent germination, radical length, and percent shoot emergence were recorded.

Results and Discussion

Figures 1-15 show the results of monthly collections of various leachates of Helianthus rigidus on germination, radical length and shoot emergence of Achillea lanulosa, Andropogon scoparius and Bromus japonicus.

The leachate from the green shoots (Figure 1) inhibited Achillea lanulosa germination during April and stimulated the germination during August and September. The radical growth and shoot emergence was not appreciably affected by the green shoot leachate. Living root leachate (Figure 2) slightly affected the germination, radical growth and shoot emergence of Achillea with both stimulation and inhibition occurring.

Dead root and litter leachates (Figures 3 and 4) moderately to significantly inhibited the germination of Achillea while the shoot emergence was generally unaffected. The radical growth was stimulated with the greatest stimulation occurring during November and December. The leachate of the dead leaves (Figure 5) was found to have the greatest



a = $p < 0.05$, b = $p < 0.01$ by χ^2 test; c = $p < 0.05$, d = $p < 0.01$ by t-test

Figure 1. Germination, Radical Growth, and Shoot Emergence of Achillea lanulosa as Influenced by Leachate From Monthly Collections of Helianthus rigidus Green Shoots

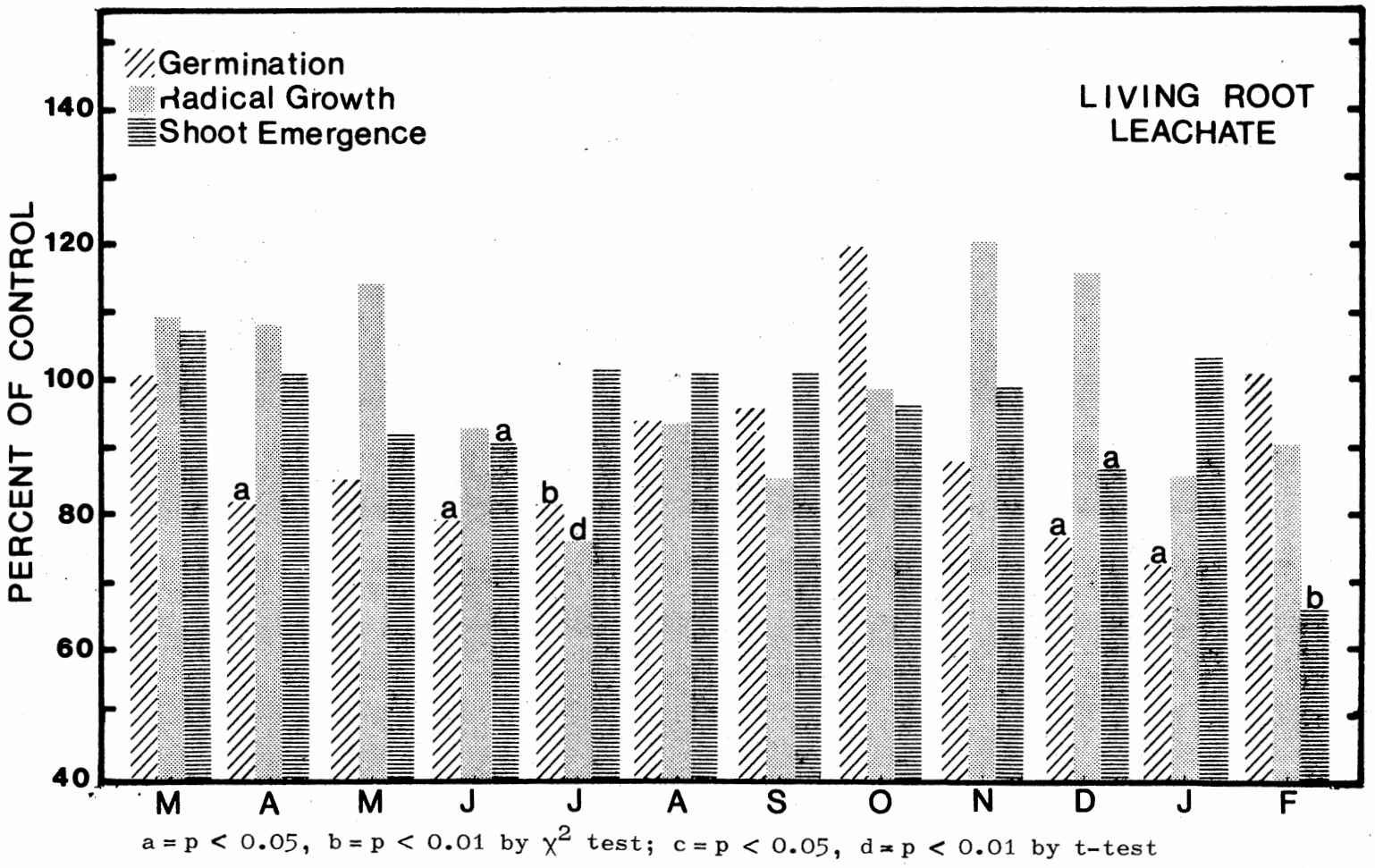
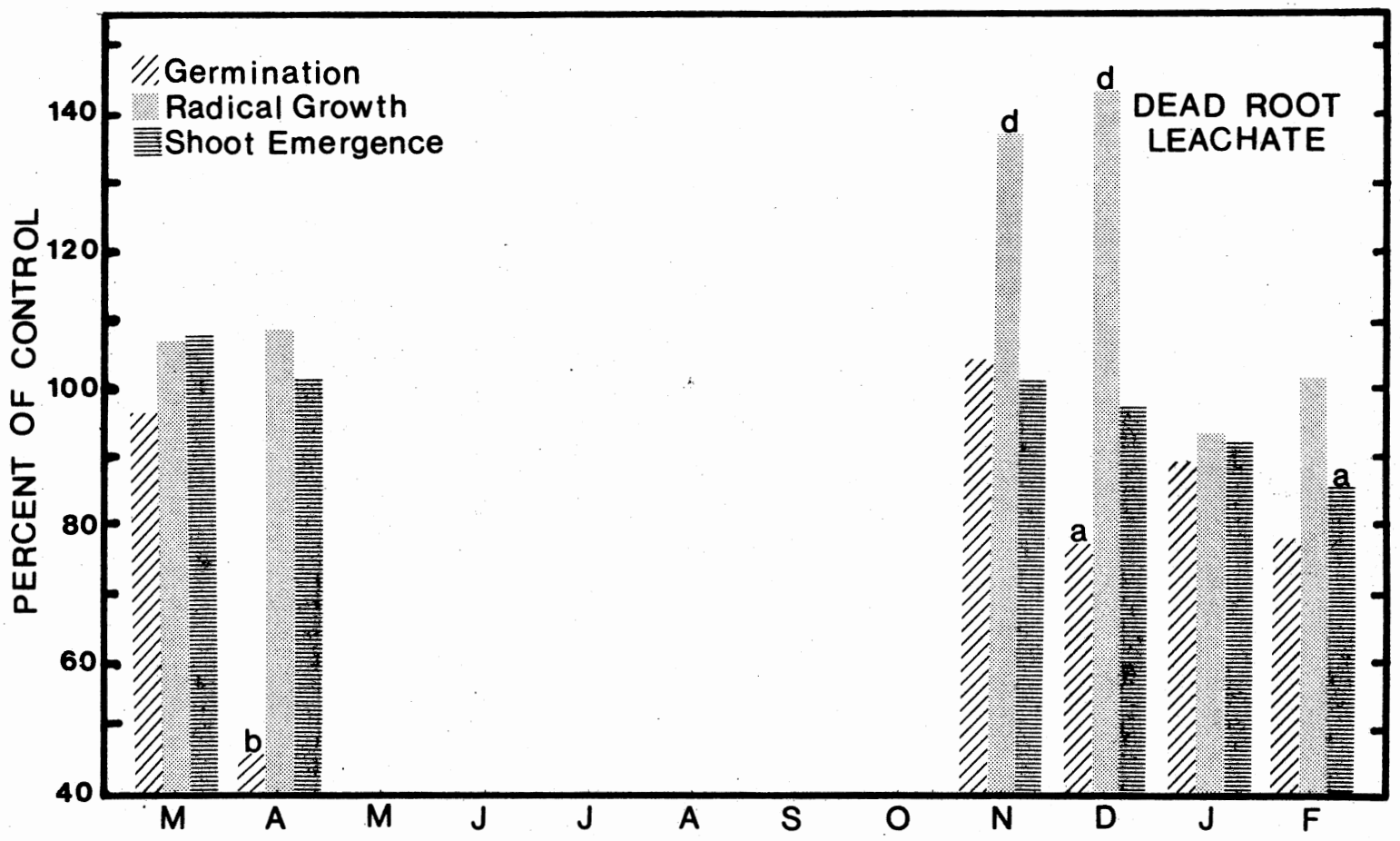
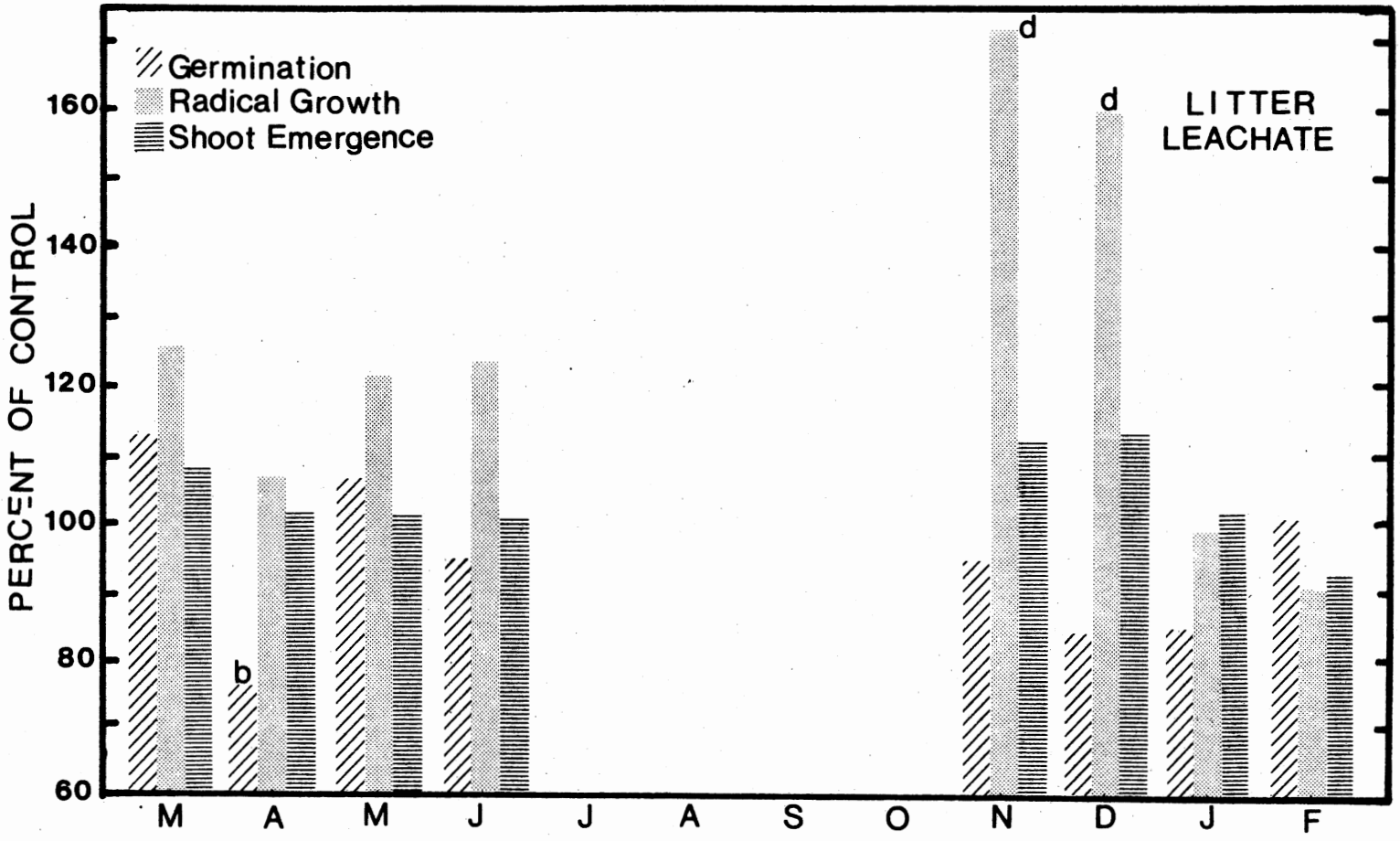


Figure 2. Germination, Radical Growth, and Shoot Emergence of Achillea lanulosa as Influenced by Leachate From Monthly Collections of Helianthus rigidus Living Roots



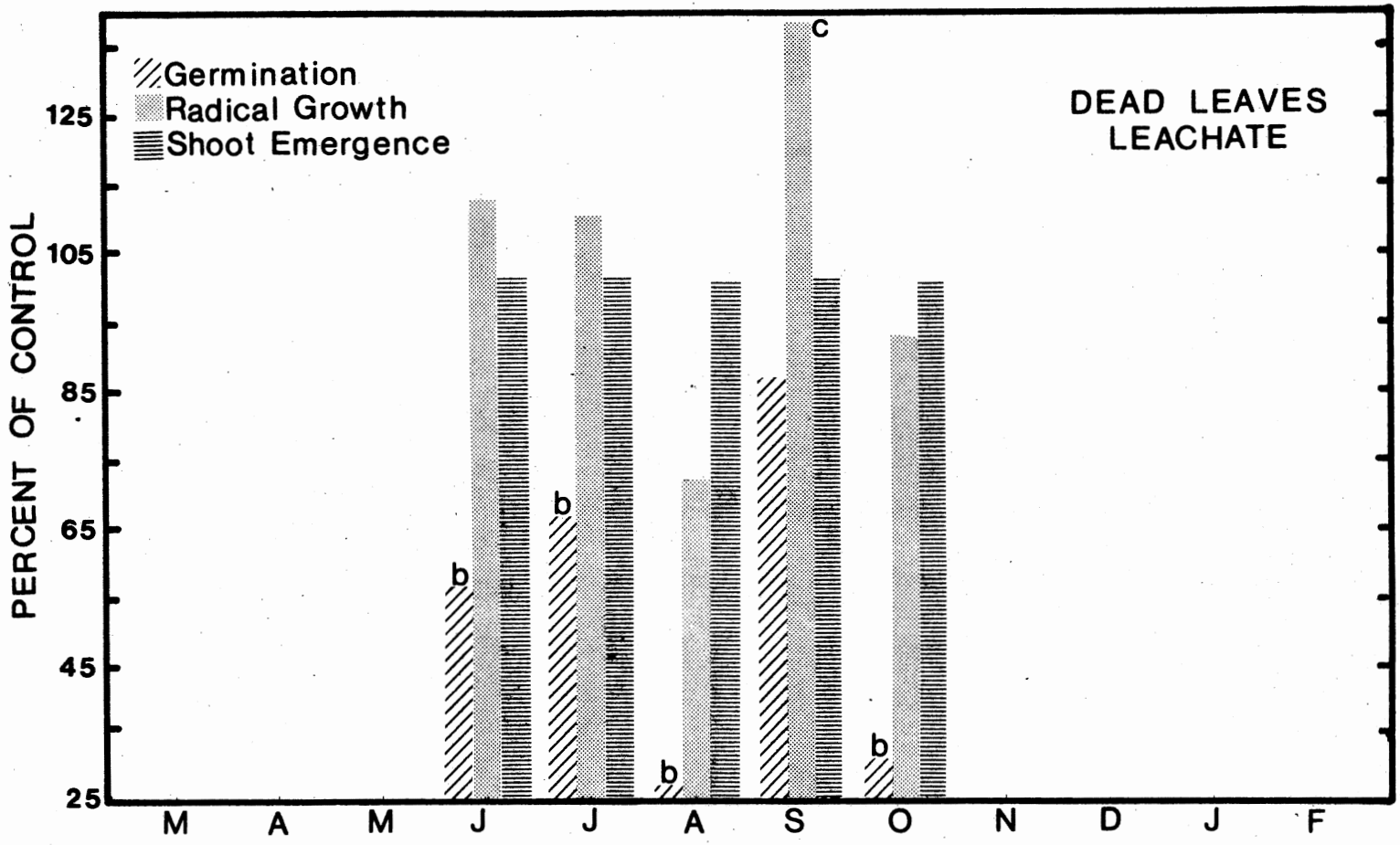
a = $p < 0.05$, b = $p < 0.01$ by χ^2 test; c = $p < 0.05$, d = $p < 0.01$ by t-test

Figure 3. Germination, Radical Growth, and Shoot Emergence of Achillea lanulosa as Influenced by Leachate From Monthly Collections of Helianthus rigidus Dead Roots



a = p < 0.05, b = p < 0.01 by χ^2 test; c = p < 0.05, d = p < 0.01 by t-test

Figure 4. Germination, Radical Growth, and Shoot Emergence of Achillea lanulosa as Influenced by Leachate From Monthly Collections of Helianthus rigidus Litter



a = p < 0.05, b = p < 0.01 by χ^2 test; c = p < 0.05, d = p < 0.01 by t-test

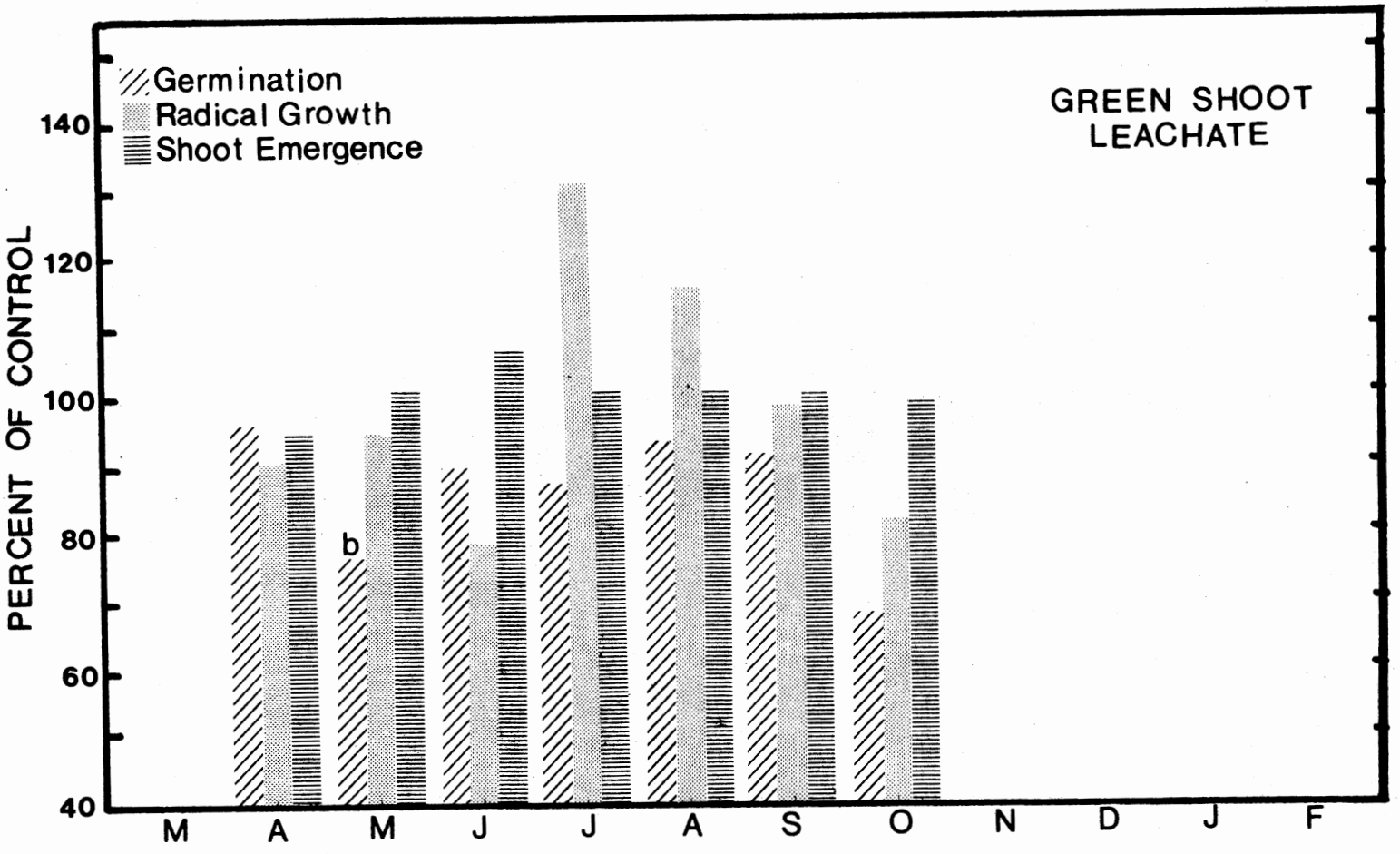
Figure 5. Germination, Radical Growth, and Shoot Emergence of Achillea lanulosa as Influenced by Leachate From Monthly Collections of Helianthus rigidus Dead Leaves

activity with the germination being significantly inhibited. The greatest inhibition occurred during August (27% of control) followed by October (31% of control) and the least inhibition occurred during September (87% of control). The shoot emergence was not affected; the radical growth was significantly stimulated during September and not affected appreciably the other times.

Leachates of Helianthus rigidus generally did not affect the shoot emergence of Achillea lanulosa; radical growth was generally stimulated. Germination was generally inhibited, except in August and September when the green shoot leachate stimulated the germination. Dead leaves leachate consistently had the greatest inhibitory affect on the germination of Achillea lanulosa.

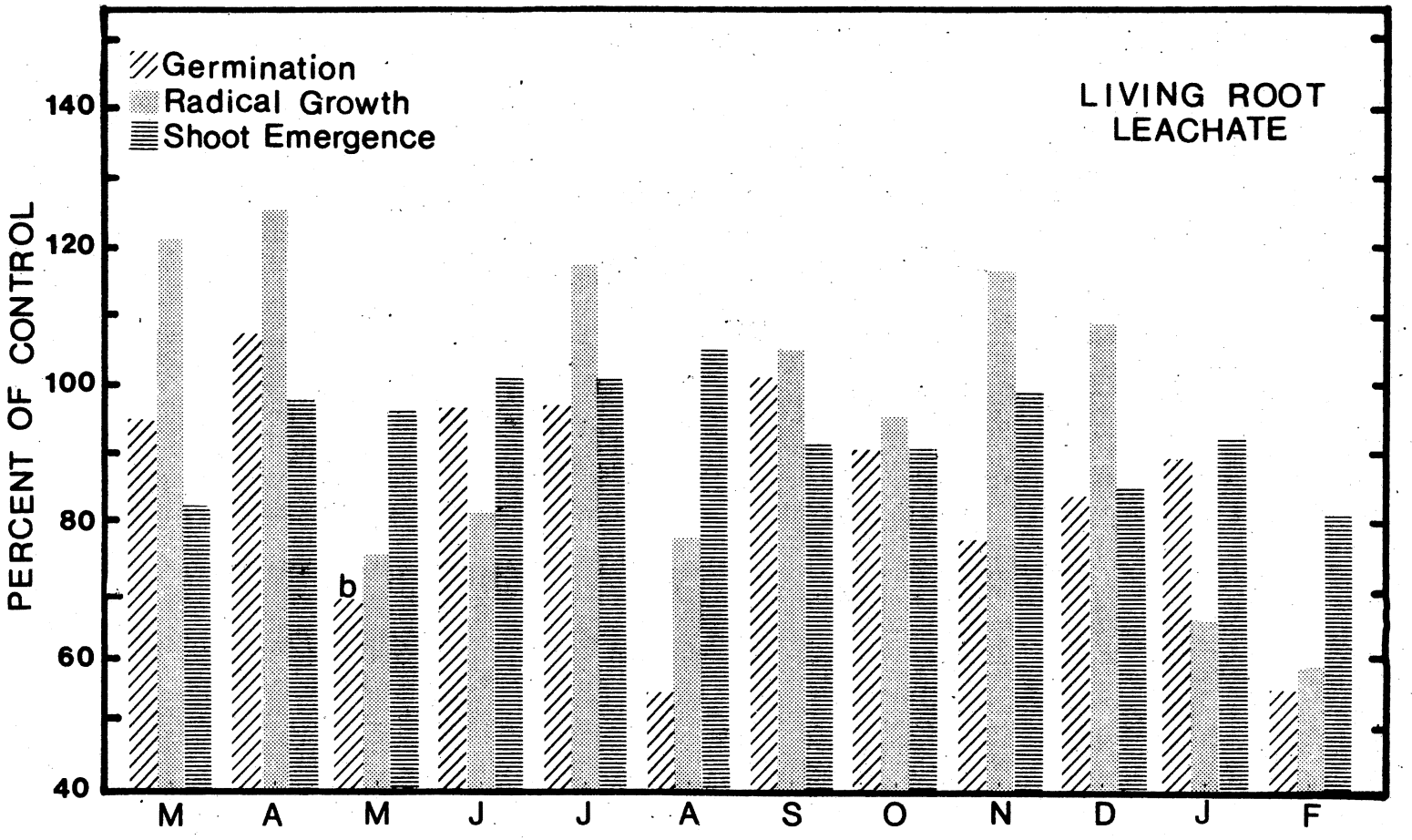
The Helianthus rigidus leachates had little statistically significant effect on Andropogon scoparius (Figures 6-10). The germination was significantly inhibited during May by leachates from green shoots, living roots and litter, and stimulated by dead leaves leachate during June. The apparent inhibition in May may have been caused by the contrast with an unusually high germination percentage in the control. None of the other responses were statistically significant and no patterns of stimulation or inhibition were observed.

Of the three test species, Bromus japonicus was the most significantly affected and varied in its response. Green shoot leachate (Figure 11) had little effect except in June when the shoot emergence was inhibited. Living root leachate (Figure 12) significantly inhibited radical growth in April, June, July, and August but stimulated it in May, November, January, and February. The shoot emergence was stimulated by living root leachate in May and inhibited in June, July, August, and October.



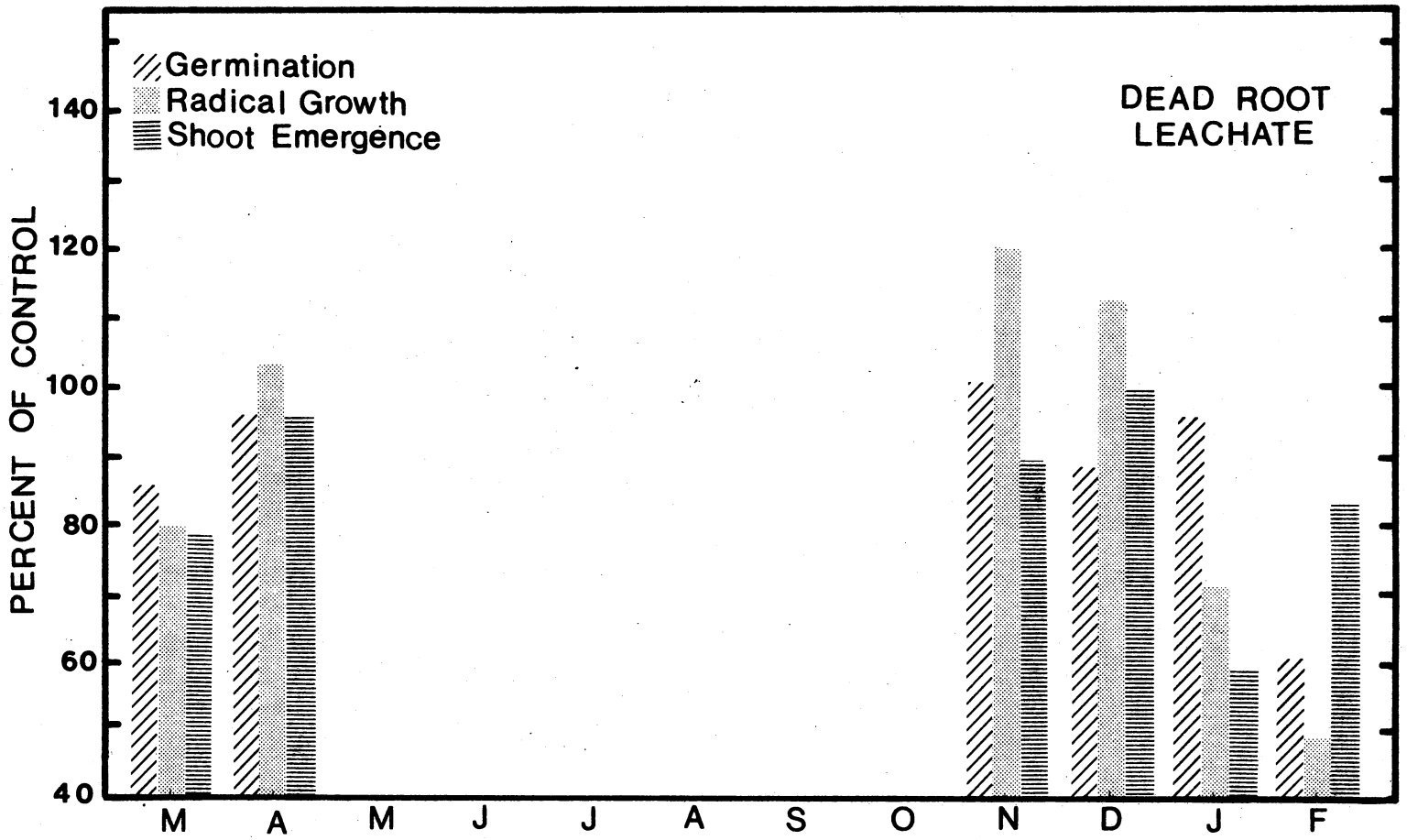
a = p < 0.05, b = p < 0.01 by χ^2 test; c = p < 0.05, d = p < 0.01 by t-test

Figure 6. Germination, Radical Growth, and Shoot Emergence of Andropogon scoparius as Influenced by Leachate From Monthly Collections of Helianthus rigidus Green Shoots



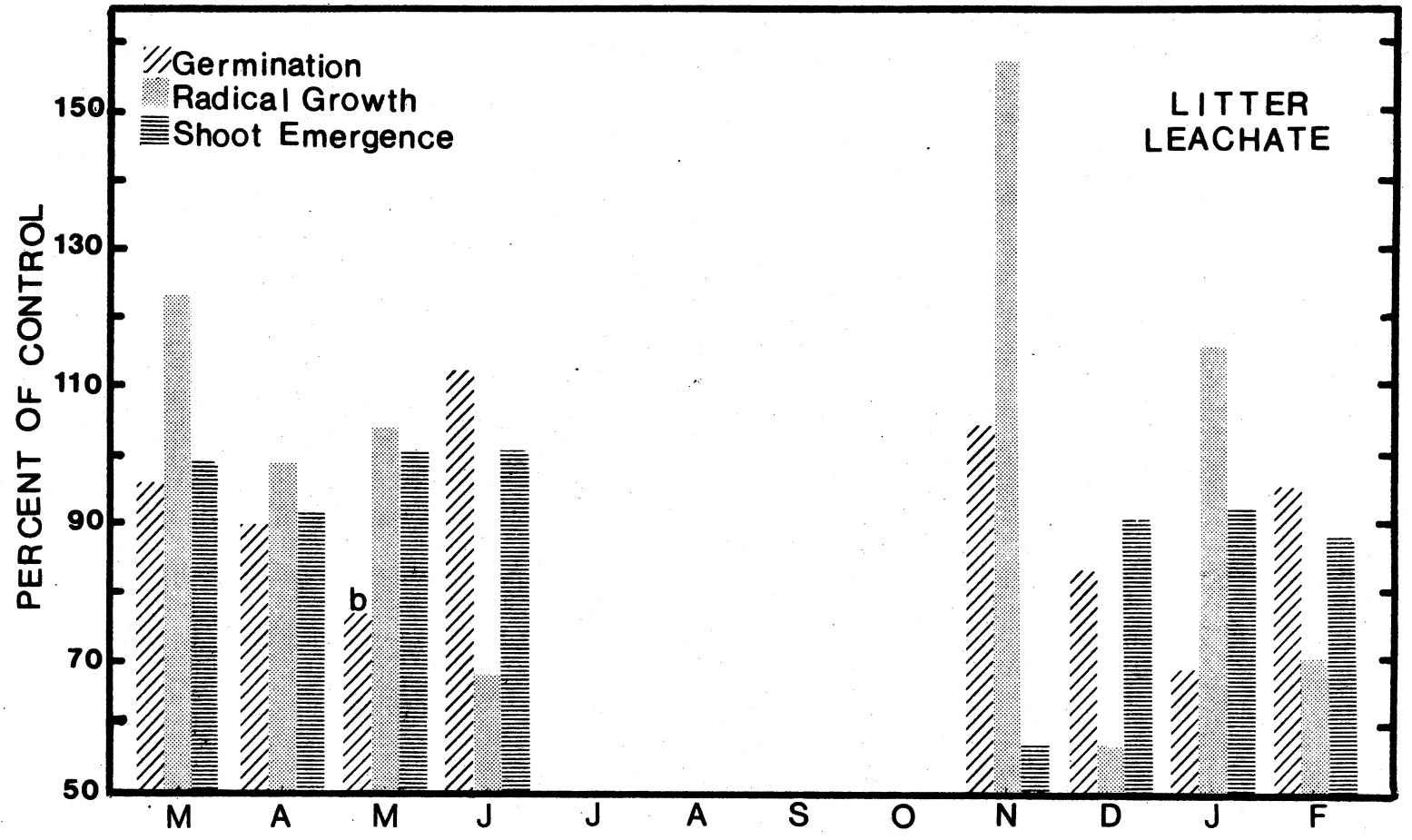
a = $p < 0.05$, b = $p < 0.01$ by χ^2 test; c = $p < 0.05$, d = $p < 0.01$ by t-test

Figure 7. Germination, Radical Growth, and Shoot Emergence of Andropogon scoparius as Influenced by Leachate From Monthly Collections of Helianthus rigidus Living Roots



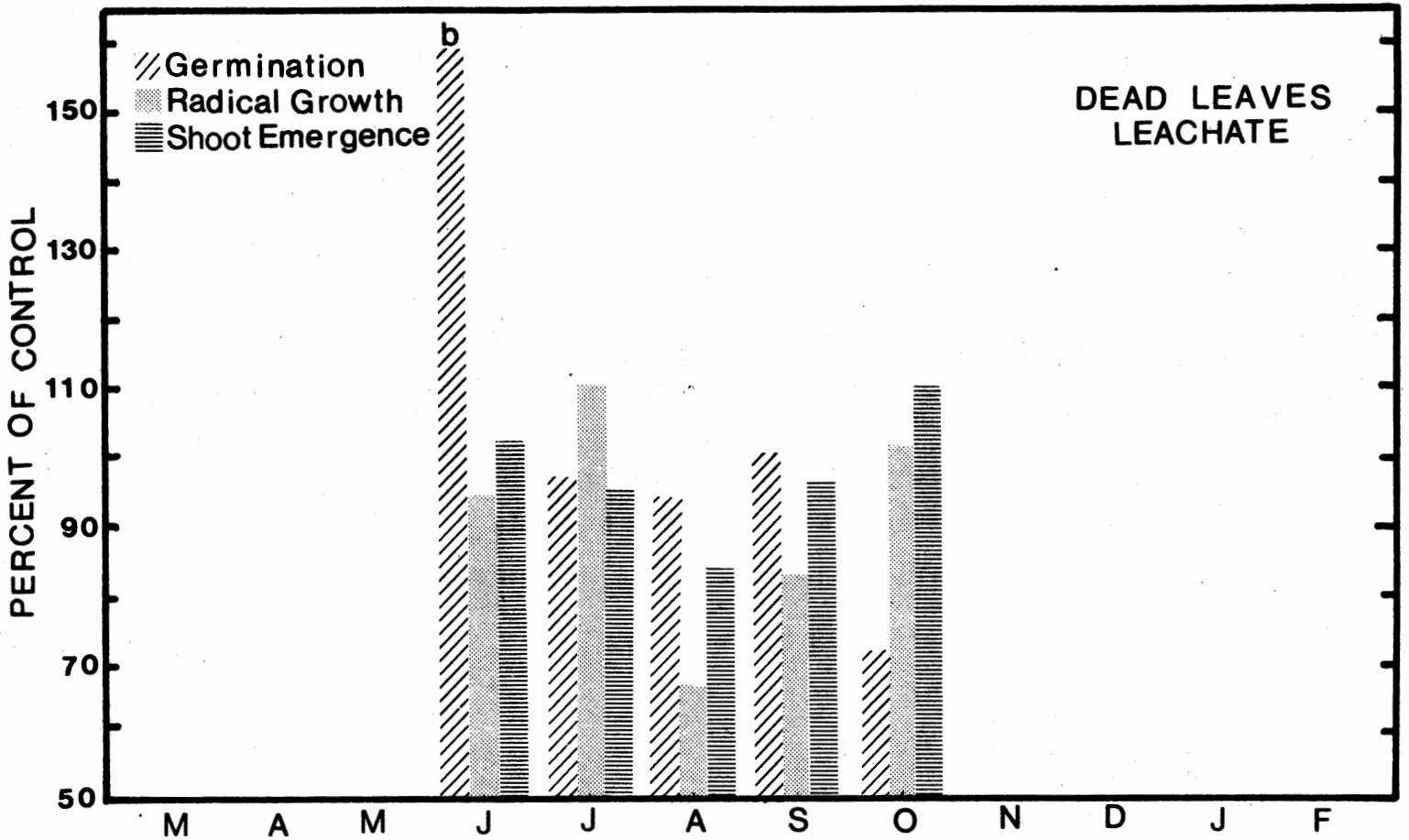
a = $p < 0.05$, b = $p < 0.01$ by χ^2 test; c = $p < 0.05$, d = $p < 0.01$ by t-test

Figure 8. Germination, Radical Growth, and Shoot Emergence of Andropogon scoparius as Influenced by Leachate From Monthly Collections of Helianthus rigidus Dead Roots



a = $p < 0.05$, b = $p < 0.01$ by χ^2 test; c = $p < 0.05$, d = $p < 0.01$ by t-test

Figure 9. Germination, Radical Growth, and Shoot Emergence of Andropogon scoparius as Influenced by Leachate From Monthly Collections of Helianthus rigidus Litter



a = $p < 0.05$, b = $p < 0.01$ by χ^2 test; c = $p < 0.05$, d = $p < 0.01$ by t-test

Figure 10. Germination, Radical Growth, and Shoot Emergence of Andropogon scoparius as Influenced by Leachate From Monthly Collections of Helianthus rigidus Dead Leaves

Leachate of dead roots (Figure 13) stimulated Bromus japonicus radical growth in February; the shoot emergence was significantly inhibited during April, December, and January. Litter leachate (Figure 14) inhibited radical growth in April, June, and February and stimulated it in December; shoot emergence was inhibited in April, June, and November through February. Dead leaves leachate (Figure 15) significantly inhibited radical growth in July, August, and October; shoot emergence was significantly inhibited from June through October with the greatest inhibition (4% of control) occurring during October. Germination was not affected by any of the leachates.

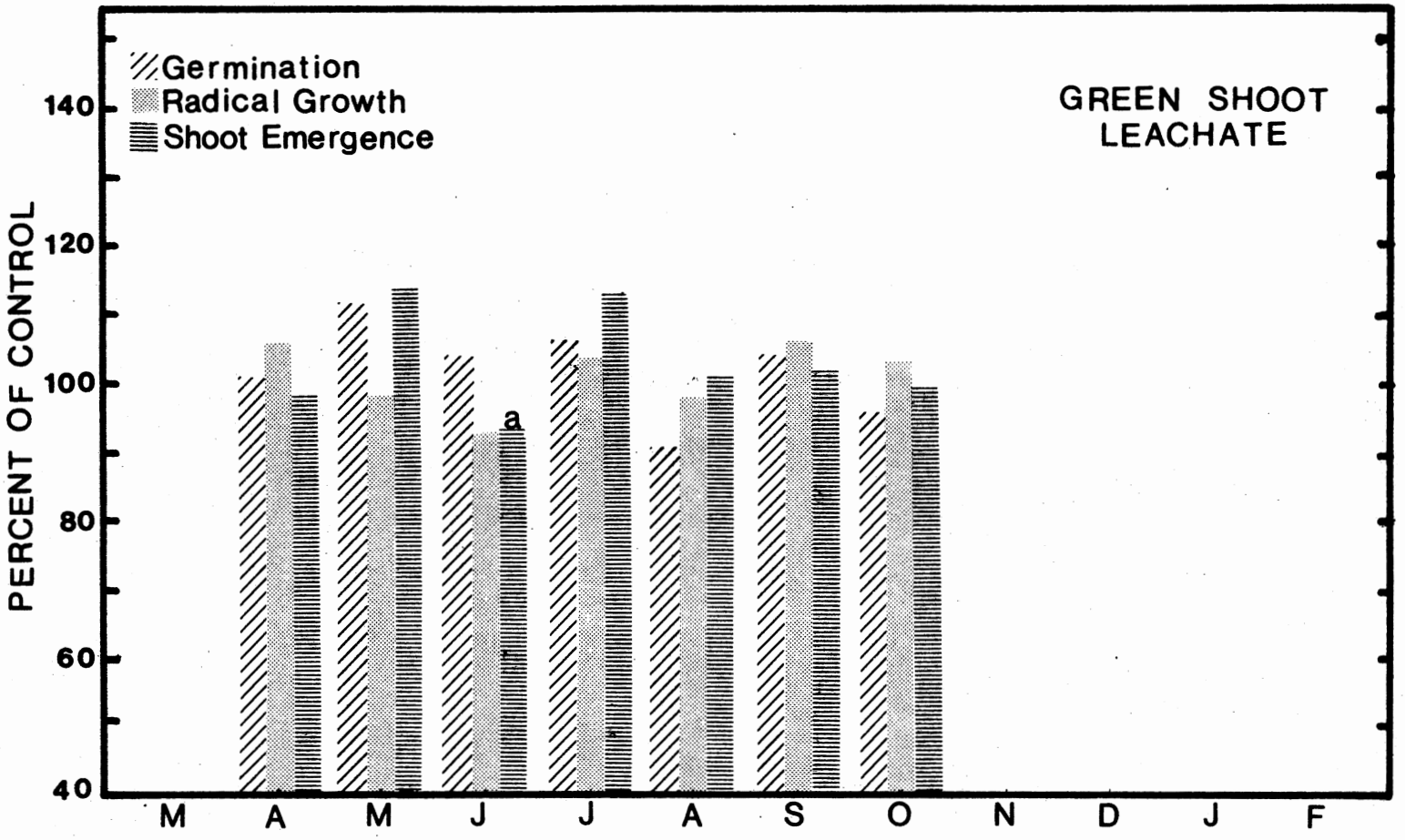
Leachates of Helianthus rigidus had no effect on the germination of Bromus japonicus. Radical growth as affected by living root leachate showed the general pattern of inhibition from April through August and stimulation from November through March.

Bromus japonicus shoot emergence was most affected by Helianthus rigidus leachates. All leachates except green shoot affected shoot emergence at least once. The living root leachate inhibited shoot emergence from June through October; litter leachate generally inhibited shoot emergence during all sampling periods. Dead leaves leachates inhibited shoot emergence during all sampling periods.

Stairstep Experiment

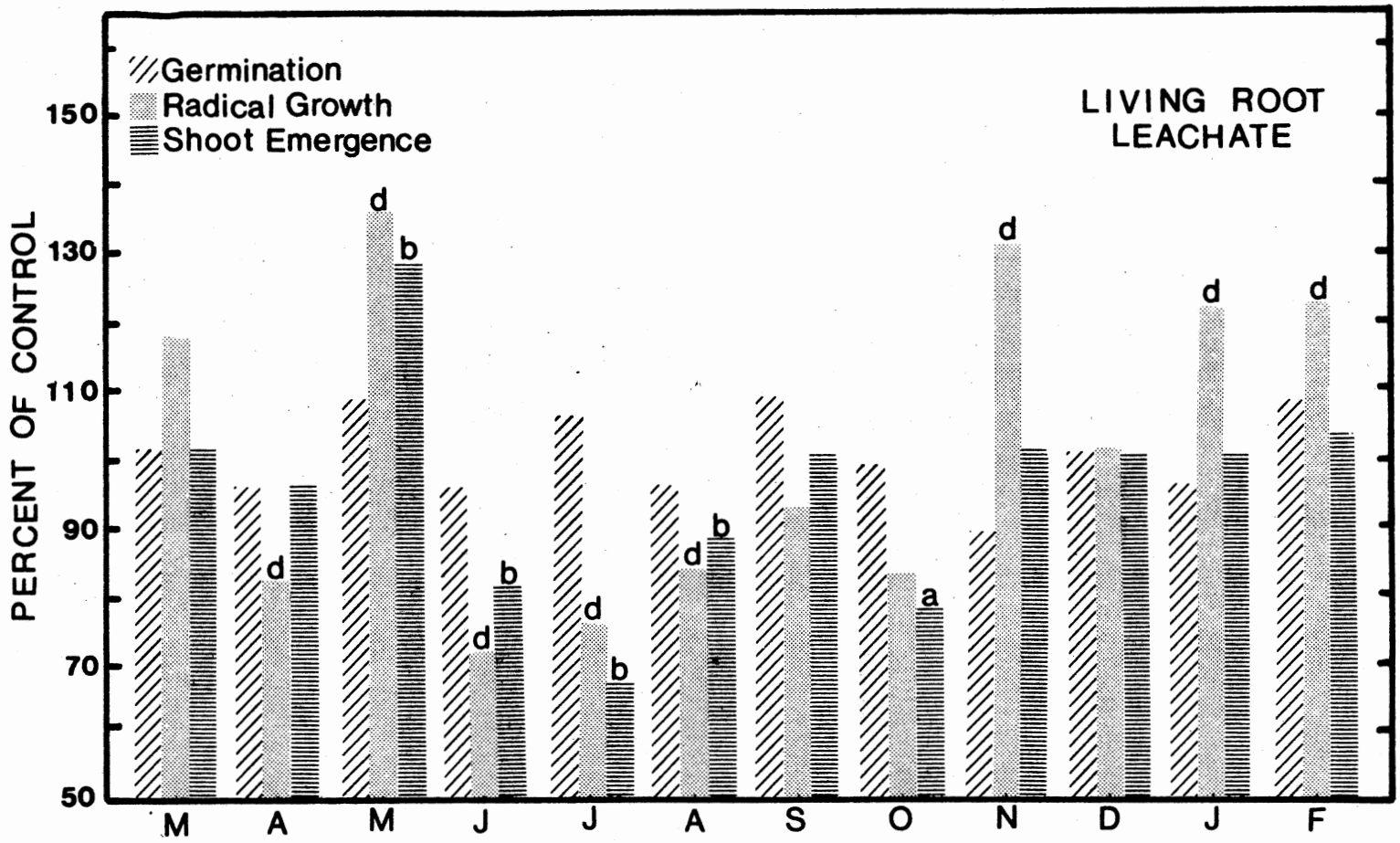
Methods of Study

The effects of Helianthus rigidus root exudates on the test species was investigated using the stairstep method described by Wilson and Rice (1968), and Bell and Koeppe (1972). This consisted of a stairstep arrangement arrangement of interconnecting pots through which a complete



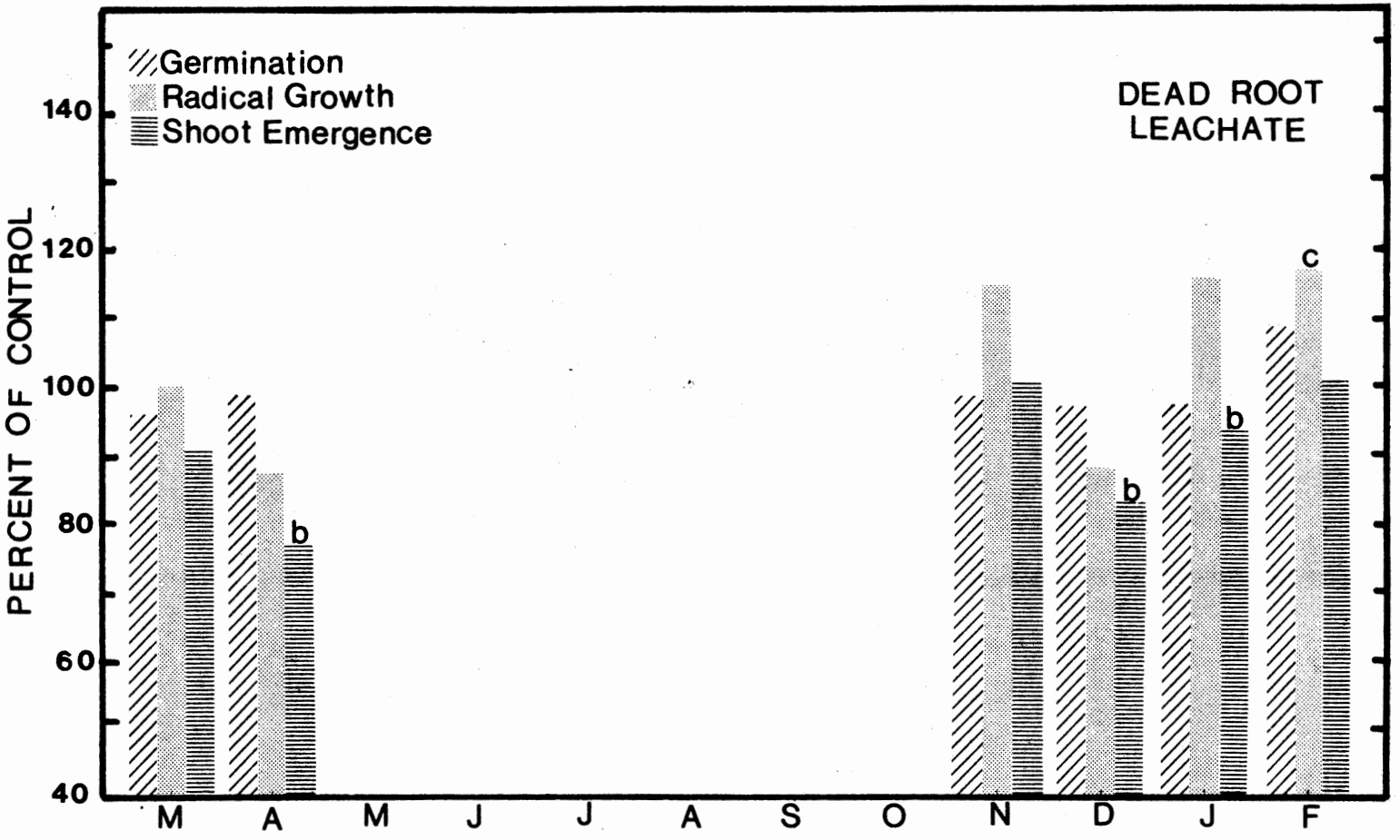
a = p < 0.05, b = p < 0.01 by χ^2 test; c = p < 0.05, d = p < 0.05, d = p < 0.01 by t-test

Figure 11. Germination, Radical Growth, and Shoot Emergence of Bromus japonicus as Influenced by Leachate From Monthly Collections of Helianthus rigidus Green Shoots



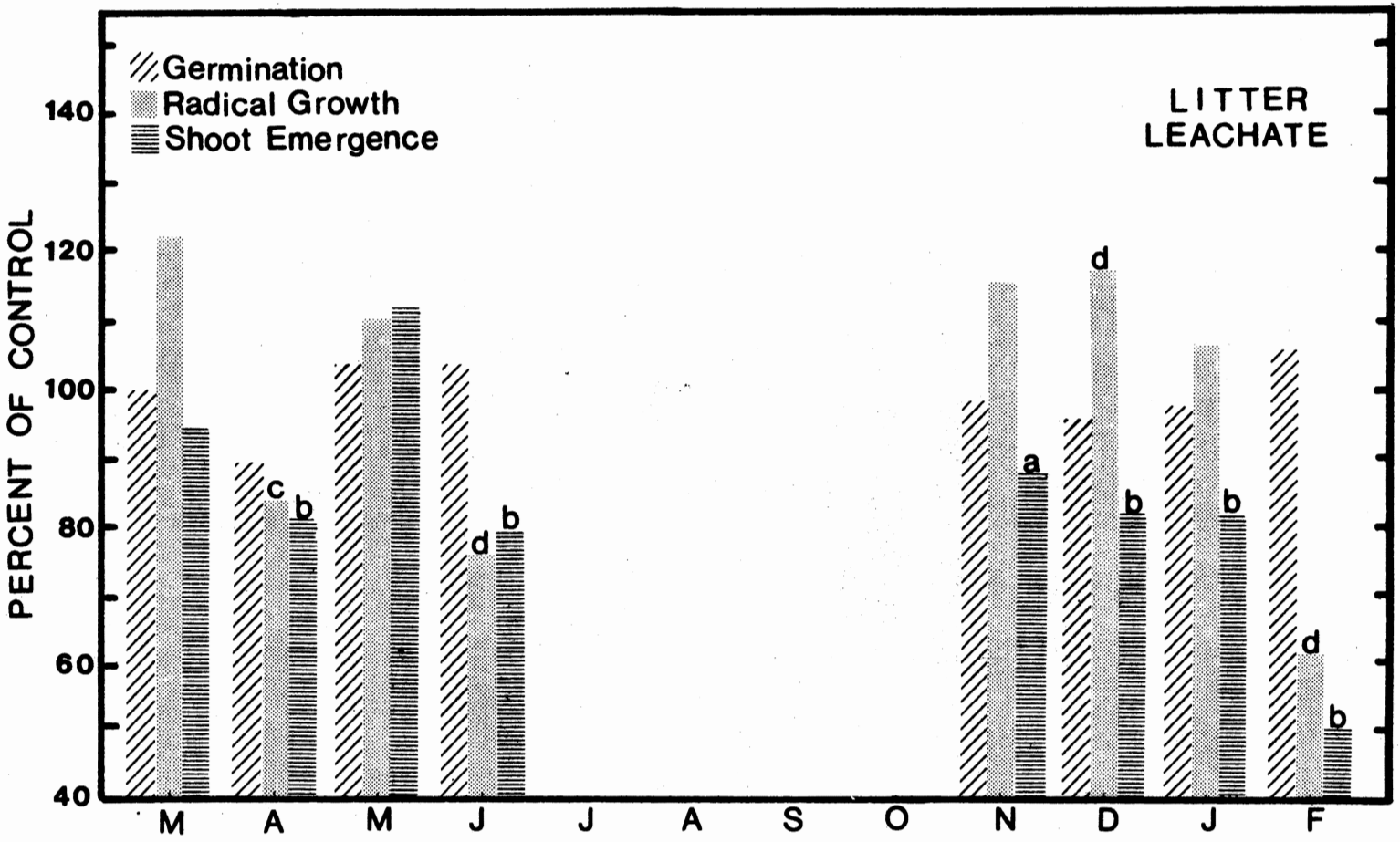
a = $p < 0.05$, b = $p < 0.01$, by χ^2 test; c = $p < 0.05$, d = $p < 0.01$ by t-test

Figure 12. Germination, Radical Growth, and Shoot Emergence of Bromus japonicus as Influenced by Leachate From Monthly Collections of Helianthus rigidus Living Roots



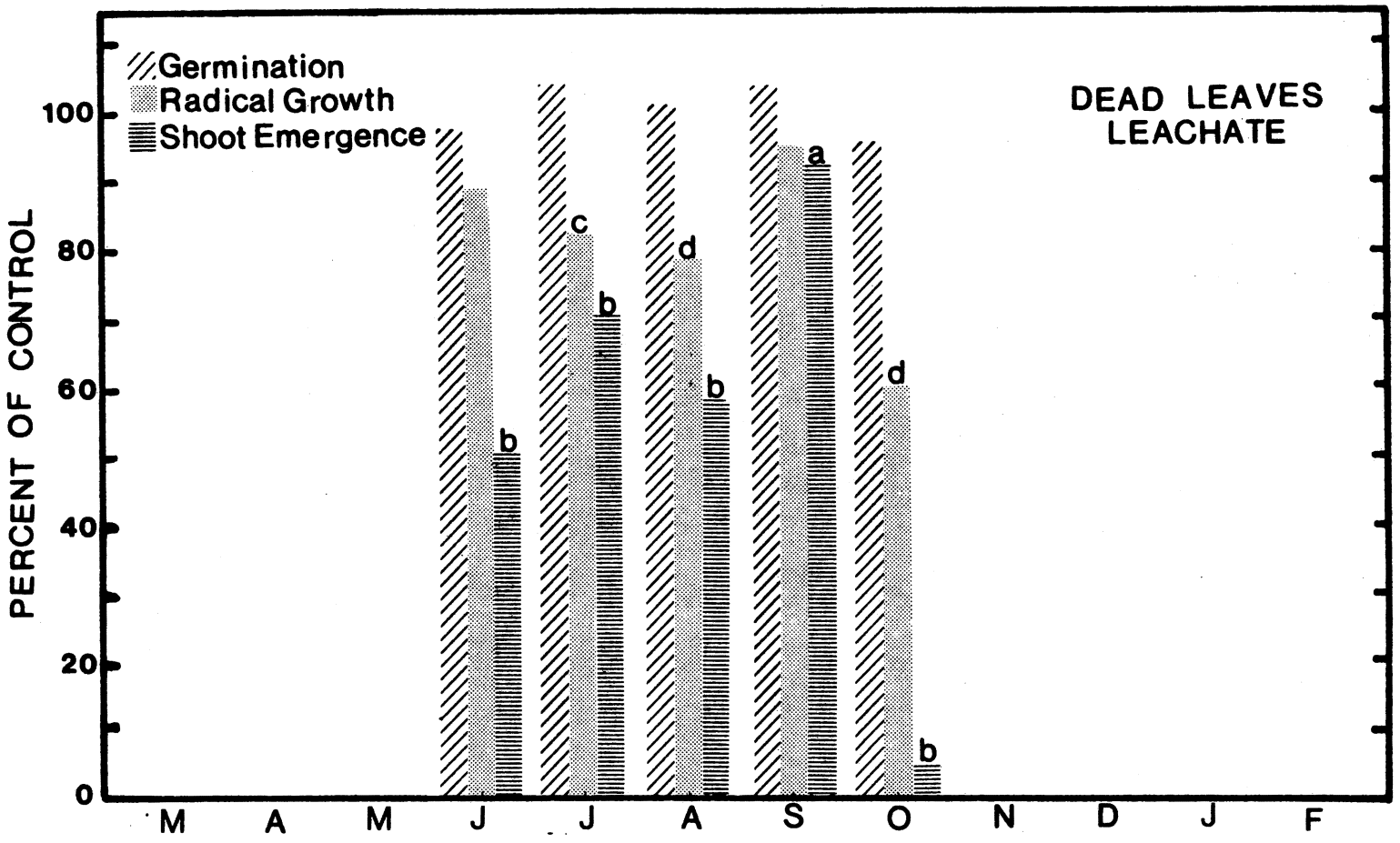
a = $p < 0.05$, b = $p < 0.01$ by χ^2 test; c = $p < 0.05$, d = $p < 0.05$, d = $p < 0.01$ by t-test

Figure 13. Germination, Radical Growth, and Shoot Emergence of Bromus japonicus as Influenced by Leachate From Monthly Collections of Helianthus rigidus Dead Roots



a = $p < 0.05$, b = $p < 0.01$ by χ^2 test; c = $p < 0.05$, d = $p < 0.01$ by t-test

Figure 14. Germination, Radical Growth, and Shoot Emergence of Bromus japonicus as Influenced by Leachate From Monthly Collections of Helianthus rigidus Litter



a = $p < 0.05$, b = $p < 0.01$ by χ^2 test; c = $p < 0.05$, d = $p < 0.01$ by t-test

Figure 15. Germination, Radical Growth, and Shoot Emergence of Bromus japonicus as Influenced by Leachate From Monthly Collections of Helianthus rigidus Dead Leaves

nutrient solution was passed. Pots were placed on a staircase which had a supply reservior at the top and collection reservior and pump at the bottom. Hoaglands nutrient solution flowed from the supply reservior through the pots in the series to the collection reservior where it was pumped back to the supply reservior. The complete cycle took approximately four hours. The water level was maintained with Hoaglands solution. This method allows the investigation of the effects of root exudates without the influence of competition.

The test series consisted of alternating pots of Helianthus rigidus and a test species. The control series consisted only of pots of the test species. Helianthus rigidus plants were grown from tubers in a three to one mixture of sand and perlite in 4 in glazed pots for four weeks. Seeds of the test species, Achillea lanulosa, Andropogon scoparius, and Bromus japonicus, after receiving the appropriate germination treatment, were planted in the same mixture of sand and perlite in 4 in glazed pots.

The germination of the test species and the height of Andropogon scoparius and Bromus japonicus were recorded after two weeks. After six weeks, the pots with the test species were removed from the stairsteps and allowed to dry. Wilting, shoot and root length, and oven-dried weights were recorded.

Results and Discussion

Table VII shows the results of the stairstep bioassay. Achillea lanulosa germination was not affected; the percent survival from second week to the sixth week was significantly decreased. The shoot length was significantly increased in the sixth week. Achillea treated with

Helianthus rigidus root excudate had more root weight per length than the control. The treated Achillea wilted more quickly than the controls.

Andropogon scoparius germination was not affected by the Helianthus rigidus root exudate; the percent survival was decreased. The shoot and root lengths and weights were increased but not significantly. The control plants wilted more quickly than the root exudate-treated plants.

Bromus japonicus germination and percent survival was not affected by the Helianthus rigidus root exudate. The shoot height was significantly increased at two weeks. At six weeks, the root length was increased but not significantly and the root weight was decreased. There was not much difference in the rate of wilting between controls and treated plants.

Helianthus rigidus root exudate did not have much effect in general on the test species. The main effects appear to be decrease in the percent survival and an increase in the root system of Achillea lanulosa and Andropogon scoparius. While in Bromus japonicus the root system appears to be decreased.

TABLE VII

GERMINATION, PERCENT SURVIVAL, SHOOT AND ROOT GROWTH, AND SHOOT/ROOT RATIO AS PERCENT OF CONTROL OF THE TEST SPECIES AS AFFECTED BY *HELIANTHUS RIGIDUS* ROOT EXUDATE

Species	2 Weeks		6 Weeks						
			%	Length			Weight		
	Germination	Shoot	Survival	Shoot	Root	Shoot/Root	Shoot	Root	Shoot/Root
Achillea lanulosa	107		73[a]	125[b]	99	80	122	123	100
Andropogon scoparius	92	75	68[a]	101	121	91	127	159	157
Bromus japonicus	104	111[c]	98	104	114	93	122	88	112

[a] $p < 0.01$ by χ^2 test

[b] $p < 0.05$ by t-test

[c] $p < 0.01$ by t-test

CHAPTER VI

PHYSIOLOGICAL RESPONSES

Laboratory experiments were initiated to investigate the effects of leachates of Helianthus rigidus on the photosynthesis of excised leaves and respiration of excised roots of Bromus japonicus. Photosynthesis was investigated with the use of $^{14}CO_2$ and a biological oxygen monitor; respiration was investigated with a biological oxygen monitor.

Photosynthesis

Methods of Study

The $^{14}CO_2$ assimulation experiment was a modification of a procedure described by Ross (1974). The leachates used in the February bioassays were used for the first investigation; the second investigation used leachates prepared in the same fashion from materials collected two weeks later. Bromus japonicus seeds were germinated and grown for twelve days in aerated distilled water at 20 C in the light, the water was changed daily. Leaf tips 2 cm long were excised and randomly floated in distilled water (control) or leachate. After two hours of treatment in the dark at 20 C, Conway dishes with leaves and $^{14}CO_2$ were placed in a 1800 fc light for 45 minutes. Photosynthesis was then stopped by the addition of acid and the leaves were extracted in boiling ethanol. The extract was counted in a 2, 4-diphenyloxazole (PPO) and 1, 4-bis 2- (5-phenyloxazoyl-benzene) (POPOP) scintillation cocktail. The second run

followed the same procedure except after two hours of treatment in the leachates the leaves were transfered to distilled water in the Conway dish before exposure to the $^{14}CO_2$ and the oven-dried weights (± 0.02 mg) of the leaves were determined.

The effect of the leachates on the oxygen evolution was determined by a biological oxygen monitor (Yellow Springs Instrument Co.). The excised Bromus japonicus leaves were grown in the same way as the $^{14}CO_2$ experiment. The excised leaves were floated on leachate or distilled water (control) at 25 C in the dark between 2-4 hours before being measured. The leaves were transfered to a partially de-oxygenated 0.05 M $NaHCO_3$ buffer, pH 6.5 in 1400 fc light for the measurement. The leachates used were from the same lots as those used in the second run $^{14}CO_2$ experiment. The second oxygen evolution experiment used leachates that had been stored at 4 C for 25 hours. After being monitored, the leaves were oven-dried and weighed to ± 0.02 mg. The readings were converted to µl O_2 evoluted/mg of leaves/min.

Results and Discussion

The results are presented in Table VIII. In the first run of the $^{14}CO_2$ assimilation experiment, the rate of assimilation in Bromus japonicus was significantly decreased by leachates of Helianthus rigidus living roots and litter. The same type of leachates, two weeks later, stimulated the rate of assimilation. This was probably due to an increase in stomatal aperature by placing the treated leaves in distilled water during exposure to the $^{14}CO_2$. The oxygen evolution was decreased by the fresh leachates, and was significantly decreased by leachates

stored 24 hours before use. Generally the photosynthesis of Bromus japonicus is decreased by February leachates of Helianthus rigidus.

TABLE VIII

$^{14}CO_2$ ASSIMILATION, OXYGEN EVOLUTION, AND OXYGEN UPTAKE OF EXCISED BROMUS JAPONICUS LEAVES AND ROOTS AS INFLUENCED BY FEBRUARY LEACHATES OF HELIANTHUS RIGIDUS AS PERCENT OF CONTROL

Leachate	$^{14}CO_2$ Assimilation		Oxygen Evolution		Oxygen Uptake	
	1st[1]	2nd[2]	1st[1]	2nd[2]	1st[1]	2nd[2]
Living Root	74[b]	131	86	33[b]	157[b]	118
Dead Root	95	93	92	53[a]	124[a]	154[b]
Litter	50[b]	152[b]	75	57	147[b]	146[b]

[1]February biossay leachate

[2]Collected two weeks after February bioassay leachate

[a]$p < 0.05$ by t-test

[b]$p < 0.01$ by t-test

Respiration

Methods of Study

Respiration was measured as a function of oxygen uptake as determined by a biological oxygen monitor (Yellow Springs Instrument Co.). The excised Bromus japonicus roots were obtained from the seedlings used in the photosynthesis experiments. The leachates were from the same

lot as those used in the $^{14}CO_2$ assimilation experiment. The excised roots were placed in the leachates or distilled water at 25 C in the dark for two to four hours prior to the measurements. In the first run the roots were monitored in the solution they had been in. In the second run the roots were transferered to distilled water for the monitoring. After being monitored the roots were oven-dried and weighed to ± 0.02 mg. The readings were converted to µl O_2 uptake/mg of root/min.

Results and Discussion

The effect of the February Helianthus rigidus leachates on the oxygen uptake of excised Bromus japonicus roots are presented in Table VIII.

The oxygen uptake was significantly stimulated by all leachates in the first run and by litter and dead roots in the second run. The degree of stimulation is generally one and one-half times of the control so the leachates are causing the Bromus japonicus roots to use the food supply faster. The stimulation of oxygen uptake was consistent with the results of some workers using purified allelopathic compounds on yeast and lettuce (Van Sumere et al. 1971). Other workers have found oxygen uptake inhibited (Koeppe 1972; Patrick and Kock 1958; Patrick et al. 1964; Muller et al. 1969).

CHAPTER VII

CONCLUSION

Helianthus rigidus appears to play an important role in the composition of plant communities and in the rate of succession. In prairie plant communities that have not reached climax, Helianthus rigidus tends to suppress the non-climax species. This tends to favor the climax species. It may also have a direct stimulatory effect on them in some cases. In climax communities, Helianthus rigidus probably contributes to the maintenance of the climax community.

In this study of non-climax communities, Helianthus rigidus clones had fewer non-climax species than the surrounding area. The species excluded from the clones were Sorghum halepense, Chaerophyllum tainturieri, Gutierrezia dracunculoides, Andropogon saccharoides and two unidentified species. Species partially suppressed by Helianthus rigidus were Achillea lanulosa, Erigeron philadelphicus, Erogrostis trichodes, Sisyrinchium angustifolium, and Sporobolus cryptandrus. The frequency, density, height, and biomass of several other non-climax species were decreased.

The climax species generally were unaffected by the increasing frequency of Helianthus rigidus although in some cases the frequency, density, height, or weight increased. Andropogon gerardi, Andropogon scoparius, Panicum vigatum, Sorghastrum nutans, and Trifolium spp. increased in frequency and density. Panicum oligosanthes var.

Scribnerianum increased in biomass, while Psoralea tenuiflora increased in height. The presence of Helianthus rigidus increases the dominance of the climax species.

The exclusion of weedy species was found not to be the result of competition for the physical factors of light, soil moisture, and soil nutrient. Field studies of light intensities within and outside Helianthus rigidus clone have shown the light intensity significantly higher within the clone. Field studies of percent soil moisture have shown the soil moisture higher to significantly higher within the clones. Laboratory studies of soil nutrients have shown wheat grown in soil from the clones to have more biomass than wheat grown in soil from the surrounding area.

Bioassays of leachates of various parts of Helianthus rigidus have shown the mode of action to be different in different test species. Of the three parameters, germination, radical growth, and shoot emergence, the leachates generally inhibited the germination of Achillea lanulosa the most, while radical growth was somewhat affected and shoot emergence was not affected. The leachates generally inhibited the shoot emergence of Bromus japonicus the most of the three parameters. The radical growth as affected by the living root leachate showed a pattern of inhibition during the summer and early fall months and stimulation during the winter months. The germination of Bromus japonicus was not affected by the leachates. Andropogon scoparius was not affected by the leachates.

Of the leachates obtained from the monthly collections of various parts of Helianthus rigidus, dead leaves remaining on the green shoot consistently inhibited at least one of the parameters. Living root, litter, and dead leaves leachates inhibited at least one of the parameters

less consistently than dead leaves and sometimes stimulated one of the parameters. Green shoot leachate had little effect on the parameters.

The different modes of action, inhibition of Achillea lanulosa germination, and Bromus japonicus shoot emergence, suggest the leachates contain a mixture of allelopathic compounds. The flunctuation in affect from month to month suggest an interaction between the compounds and their concentration. The effects vary as the concentrations vary.

Helianthus rigidus root exudate reduces the survival of seedlings of Achillea lanulosa and Andropogon scoparius. The root exudate increases the amount of branching in the root system of Achillea lanulosa and Andropogon scoparius and decreases the amount in Bromus japonicus.

The February leachates of Helianthus rigidus inhibited the $^{14}CO_2$ assimilation, and oxygen evolution of excised Bromus japonicus; the oxygen uptake by excised roots was stimulated. If a plant is stimulated to use its food reserves faster than they are being produced, than that plant will not be able to survive in that environment. Living root and dead roots leachates stimulated the radical growth in the bioassay and stimulated oxygen uptake; litter leachate inhibited radical growth and stimulated oxygen uptake. These again indicates the complexity of the leachates and the mode of action of the allelopathic chemicals.

Although this study has not produced strong conclusive evidence for allelopathy, strong evidence has been presented that the interference of Helianthus rigidus is not competition. Some of the reasons that this study did not present strong evidence for allelopathy are: The test species used might not be as susceptible as other species; the paramenters monitored might not be the ones the allelopathic

chemicals are affecting; the genetic make-up of the clone furnishing the material for the bioassays might have produced smaller-than-normal amounts of the chemicals; the substances produced by Helianthus rigidus might have to be acted upon by bacteria before they are effective.

Another possibility is the effect on the nitrogen cycle. Several weedy species have been shown to inhibit nitrogen-fixation and nitrification (Rice 1964). The order of succession has been shown to follow the nitrogen requirements of the species (Rice et al. 1960). Thus if Helianthus rigidus produced a substance that either stimulated nitrogen fixing bacteria or deactivated the inhibitors, the nitrogen concentration would increase promoting the growth of climax species. This increase in nitrogen would help explain the increase in growth of wheat plants grown in the clone soil.

In conclusion, Helianthus rigidus plays an important role in the plant community and the rate of succession even though the mechanisms of this role are not completely understood.

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